UNIVERSITY OF HAWAII
LIBRARY
SEP 25 '50

VOLUME X NUMBER 7

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Contents

TAXONOMY, SYSTEMATIC BOTANY AND BIOSYSTEMATICS, *Herbert L. Mason* .. 193

POLYPLOIDY IN ECHINOCYSTIS, *Thomas W. Whitaker* 209

IRA WADDELL CLOKEY, *Herbert L. Mason* 211

A GRAPHIC REPRESENTATION OF BESSEY'S TAXONOMIC SYSTEM, *R. Lucas Rodriguez C.* 214

DIOECIOUS MELANDRIUM IN WESTERN NORTH AMERICA, *H. G. Baker* 218

REVIEW: A. S. Crafts, H. B. Currier, and C. R. Stocking, *Water in the Physiology of Plants* (Leonard Machlis) 222

Published at North Queen Street and McGovern Avenue
Lancaster, Pennsylvania

July, 1950

MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

Board of Editors

Herbert L. Mason, University of California, Berkeley, Chairman.
LeRoy Abrams, Stanford University, California.
Edgar Anderson, Missouri Botanical Garden, St. Louis.
Lyman Benson, Pomona College, Claremont, California.
Herbert F. Copeland, Sacramento College, Sacramento, California.
Ivan M. Johnston, Arnold Arboretum, Jamaica Plain, Massachusetts.
Mildred E. Mathias, Dept. of Botany, University of California, Los Angeles 24.
Bassett Maguire, New York Botanical Garden, N. Y. C.
Marion Ownbey, State College of Washington, Pullman.

Secretary, Editorial Board—Annetta Carter
Department of Botany, University of California, Berkeley
Business Manager—Rimo Bacigalupi
North Queen Street and McGovern Avenue, Lancaster, Pennsylvania
or
Natural History Museum,
Stanford University, California

Entered as second-class matter October 1, 1935, at the post office at Lancaster, Pa., under the act of March 3, 1879.

Established 1916. Published quarterly. Subscription price $3.50 per year. Completed volumes I to VIII, $5.00 each; volume IX, $6.00; succeeding volumes, $7.00; single numbers $1.00.

Papers up to 15 or 20 pages are acceptable. Longer contributions may be accepted if the excess costs of printing and illustration are borne by the contributor. Range extensions and similar notes will be published in condensed form with a suitable title under the general heading "Notes and News." Articles may be submitted to any member of the editorial board. Manuscripts may be included in the forthcoming issue provided that the contributor pay the cost of the pages added to the issue to accommodate his article. Reprints of any article are furnished at a cost of 4 pages, 50 copies $7.04; 100 copies $7.73; additional 100's $1.46; 8 pages, 50 copies $10.21; 100 copies $11.33; additional 100's $2.24; 16 pages, 50 copies $14.32; 100 copies $16.04; additional 100's $3.34. Covers, 50 for $4.72; additional covers at $2.84 per hundred. Reprints should be ordered when proofs are returned.

Published at North Queen Street and McGovern Avenue, Lancaster,
Pennsylvania, for the

CALIFORNIA BOTANICAL SOCIETY, INC.

President: LeRoy Abrams, Stanford University, California. First Vice-President: Lincoln Constance, University of California, Berkeley, California. Second Vice-President: Elizabeth McClintock, California Academy of Sciences, San Francisco. Secretary: Phyllis D. Gardner, Department of Botany, University of California, Berkeley. Treasurer: Rimo Bacigalupi, Natural History Museum, Stanford University, California.

Annual membership dues of the California Botanical Society are $3.50, which includes a year's subscription to Madroño. For two members of the same family the dues are $4.50, which includes one copy of Madroño and all other privileges for both. Dues should be remitted to the Treasurer. General correspondence and applications for membership should be addressed to the Secretary.

TAXONOMY, SYSTEMATIC BOTANY AND BIOSYSTEMATICS

Herbert L. Mason

Before me are copies of several works in which are used the terms "Taxonomy," "Systematic Botany," "Biosystematics," and "Experimental Taxonomy." They include works by such authors, among the botanists, as Linnaeus (1753), De Candolle (1813), Lindley (1830, 1853), Le Maout and Descaisne (1876), Radlkofer (1883) and his student Solereder (1899), Engler and Gilg (1924), Wettstein (1924), Hall and Clements (1923), Bremekamp (1939), Turrill (1942), Gilmour and Turrill (1941), Benson (1943), Clausen, Keck and Hiesey (1939, 1940), Camp and Gilly (1943), and among the zoologists such writers as Dobzhansky (1941) and Ernst Mayr (1942). I seek an understanding of the scope of Plant Taxonomy in terms of its organization, the sources of its materials, its research methods and its objectives. More particularly, I seek to understand whether Taxonomy, Systematic Botany and Biosystematics have any separate and independent standing or whether they are to be regarded as wholly or partially synonymous with each other. For the most part, I am not searching for definitions: I am interpreting usage, oftentimes over and above, or in spite of definition, for it is usage and the history of usage that ultimately molds the meanings of our words and terms. I am familiar with the current concepts of plant taxonomy and how its scope and its methodology have grown with the advancement of the science of Botany. I know the confusion in the literature, and in the minds of botanists, between the terms "Taxonomy" and "Systematic Botany." And I have grown up along-side of Biosystematics and have shared the enthusiasm of its workers, am aware of its values, and know something of its limitations. Let me make it clear that I write not as an authority who would seek to impose what may seem to be his somewhat arbitrary views upon the uninformed but rather as one who has given the subject long and serious thought and who now wishes to present his tentative conclusions to open forum for discussion.

The word "taxonomy" was given us by the elder De Candolle. He used it as a heading for a part of "Theorie Elementaire" with the subheading "Theorie de Classification," a phrase which he presented in the text as a definition of taxonomy. However, he oriented the principles of taxonomy toward seeking a basis of resemblance (symmetry) among plants in order to explain their "relationship." Relationship was thought of solely in terms of the community of characteristics that accounted for resemblance. His principles, although not entirely acceptable today, were largely those of a systematic approach to comparative morphol-

---

Madroño, Vol. 10, No. 6, pp. 161–192. May 2, 1950.

ogy, chiefly organography. In later chapters, he discussed natural arrangement, the concept of the taxonomic categories, and phytography, which has been termed the art of description, and included in it what we today term nomenclature and synonymy. Thus the classical taxonomy was concerned with classification and the establishment of relationship and used as its major tools comparative (systematic) morphology as the source of fact, a system of taxonomic categories, a system of nomenclature, and precise description.

There is no doubt but that the tangible product of the labors of such men as De Candolle was a system of classification, but in view of the principles outlined by him and the logic of their arrangement, it is also perfectly clear that the system of classification did not stand as the end and objective of taxonomy but rather through its arrangement into a system of inclusive categories, and its nomenclature it served as the vehicle of expression of the relationship that the taxonomist sought to depict. Thus the system of classification, rather than solely an end, is also a tool of the taxonomist. It is his working hypothesis. It seems clear then that from the beginning of taxonomy, the stage was set for a clear differentiation between the overall objectives of taxonomy and the tools it fashioned and established to achieve its ends. These tools included a source of, and a method of arriving at facts, and a method of presentation or arrangement of these facts to express the relationships among plants. Thus from the beginning Taxonomy was a synthesis of facts into an expression of botanical interrelationships.

I have not as yet established just where and with whom the term "Systematic Botany" originated. From its early use, it must have followed very closely upon the term "taxonomy" and might possibly have even preceded it. Lindley used it in 1830 but seems not to have mentioned it in the 1853 edition of "The Vegetable Kingdom" in which he gave an elaborate survey of the history of taxonomy. Certainly the term "systematic" pertained to the "System" and presumably the "Natural System." Its early use seems to have been as a casual self-evident term, but later definitions associated it with seeking the evidence of relationship and this must mean the relationship that is associated with community of characters rather than the phylogenetic relationship which followed the theory of evolution. It was not until the effective application of the methods of the plant anatomists to taxonomy under the impetus of Radlkofer that we find the term used with enthusiasm. Here, quite definitely, it was used in the sense of a "new Taxonomy" with Systematic Anatomy as its major tool. Taxonomy, however, is ageless; there is no old and no new Taxonomy. There are, however, new methods of arriving at facts and new integrations possible from time to time and it is these new methods that constitute the new Taxonomy of succeeding generations of botanists. Radlkofer and his students defined "Systematic Botany" much in the sense we have outlined Taxonomy as established though usage by De Candolle and his contemporaries. These plant anatomists, however, emphasized arriving at relationships and left for Taxonomy only classification and nomenclature. They glorified the anatomical method as the true method of determining relationship yet, in effect, many but not all of them accepted the system of the early taxonomist and in an orderly manner built up an enormous volume of fact about each systematic group of plants without at the same time utilizing these facts to establish relationship. The type example is the magnificent work of Solereder, "The Systematic Anatomy of the Dicotyledons." Here the anatomical method is not used to build a system of classification, as one would suppose from Solereder's introduction, but rather the working hypothesis of Bentham and Hooker was accepted as a method of approach to the subject of Systematic Anatomy. Solereder's work stands in its own right as a solid and valuable contribution to Plant Anatomy and to Taxonomy. If we accept the usage of Solereder, this is his Systematic Botany in spite of his definition, and it can be put to any use to which the facts of Comparative Anatomy may be utilized. Such a Systematic Botany is enormously valuable to Taxonomy by virtue of the accumulation of facts along a systematic pattern. It is "systematic" primarily by virtue of canvassing, however thoroughly, the anatomical features of the system. It is a method of arriving at comparable facts and is indispensable to the taxonomist in testing his hypotheses. Whereas it can and must be utilized to the fullest by the taxonomist, it certainly is not synonymous with Taxonomy.

Because of the confusion in the literature relative to the terms Systematic Botany and Taxonomy, it may seem now to be a matter of arbitrary choice as to which we shall accept for the classical Taxonomy. I would choose the older term "Taxonomy" for this role for, if we accept the term Taxonomy in the sense of the usage of those who use "Systematic Botany" in the broader sense, then what is here considered under the heading of Systematic Botany will either have to be considered under Taxonomy, in a restricted sense, or a new term created for it. It is desirable to keep it separate because its conclusions are wholly objective and fully documented in contrast to those aspects here considered under the Taxonomic System, which are almost wholly subjective and involve interpretation in terms of concepts of taxonomic categories and of phylogenetic series of morphological characters. Systematic Botany, as I see it, involves research techniques and a research point of view that uncovers facts which may also be utilized independently of any taxonomic usage. I have found no evidence that Taxonomy ever has been used in this particular restricted sense while certainly Systematic Botany was so used even though the authors who so used it defined it in a broader sense, a sense they did not adhere to in their own work.

With the development of the various branches of Botany to the point that a systematic approach to their problems will yield fruitful results, there will be an increasing need for the term "Systematic Botany," used in the precise sense in which Solereder em-

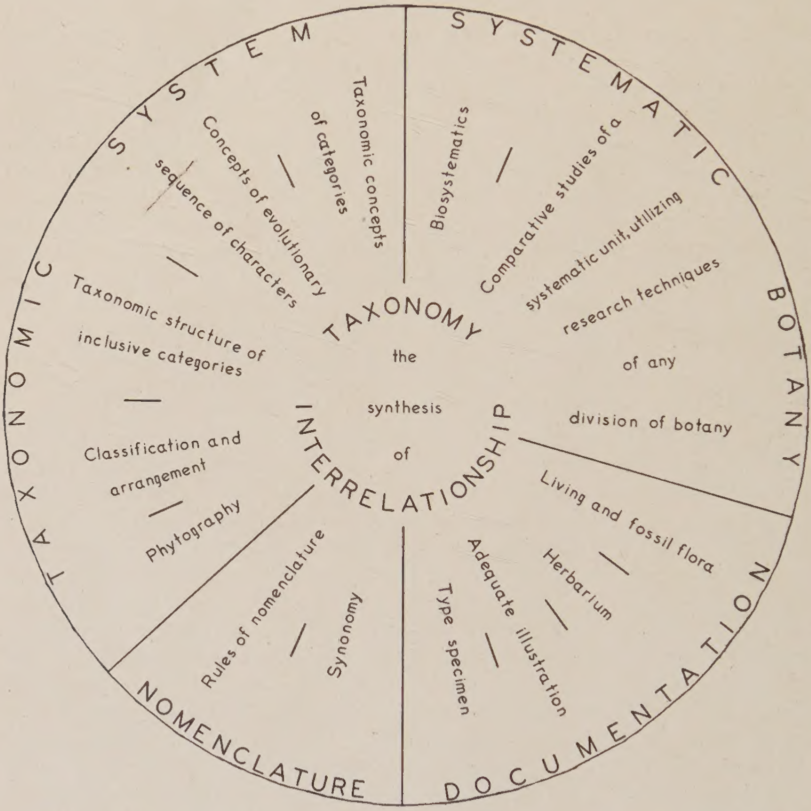


FIG. 1. The organization of the science of Taxonomy. Four fields are represented. The field of research and investigation (the fact-finding processes) are centered in Systematic Botany. The facts so determined are assembled and classified according to concepts of the evolutionary sequence of characters and organized into the series of inclusive categories. These categories are then arranged in the taxonomic structure in such a way as to give expression to the pattern of relationship. A system of nomenclature is employed according to rules, and superfluous names are relegated to synonymy. The botanical facts and the nomenclature are documented by 1) the flora of living and fossil plants, 2) the herbarium, 3) the type specimen or, 3a) by adequate illustration. Each segment of the diagram constitutes a significant tool of Taxonomy and plays a part in this synthesis of interrelationship.

ployed it. Already we see evidence of a rapidly formulating Systematic Cytology and a Systematic Genetics. Some significant beginnings have been made in a Systematic Biochemistry. "Comparative Botany" (Comparative Anatomy and Comparative Morphology, etc.) is not adequate to the needs of Taxonomy unless it presents a systematic comparison. The comparison, to be significant, must be throughout a systematic group. The connotation of a "systematic group" is significant to the concept of Systematic Botany and of Taxonomy because of the implication of relationship. It is an implication that the systematic approach to a basic discipline is designed to test. The systematic approach to each of the divisions of Systematic Botany will yield documented facts that may be of use to the taxonomist in his synthesis of interrelationships. They constitute the materials for a method of pitting the facts of one discipline against those of another to test hypotheses of relationship. We may define Systematic Botany as the comparative study of any related (systematic) group of plants utilizing the research techniques of any of the divisions of botany. In contrast, Taxonomy is the synthesis of all of the facts about plants into a concept and expression of the interrelationships of plants. Systematic Botany is its major source of botanical fact.

At the time of De Candolle, only Comparative Organography had accumulated a sufficient body of fact and methodology about it to enable systematic studies to be fruitful. Later, Comparative Anatomy reached a point where certain additional but limited systematic approaches were available. It was not until near the end of the first quarter of the current century that Cytology and Genetics jointly found themselves in a position to approach their field from the point of view of systematics, and Taxonomy finds the results of this work of very great significance. Further advances in the investigations of the vascular anatomy of flowers and of the anatomy of stems and leaves have provided new facts and methods of value to Taxonomy. It is significant that the theory of evolution completely revolutionized the point of view in Taxonomy and gave direction and clear meaning to the concept of relationship but it did not immediately provide additional facts. It resulted only in the reconsideration of those facts already established. Since community of characteristics serves as the evidence of relationship under the evolutionary concept as it did under the natural systems, certain putatively phylogenetic systems differ little from the older natural systems, and all are strikingly alike in many of their details. The chief differences between modern systems result from differences in point of view in interpreting developmental trends in the evolution of morphological characters.

It should be pointed out that Taxonomy can advance only to the extent that the basic fields of research in botany upon which it rests have accumulated documented, comparable facts of utility to the taxonomist. Should these fields go to sleep or fail to awaken, Taxonomy must also sleep. During such time [illegible]onomy may be brought up to date but it cannot advance.

There has recently come into prominence a new term, [illegible]ly, Biosystematics, and it has been hailed as the "New Taxon[illegible] appears to have been the case with the term "Systematic[illegible] that preceded it. This over-emphasis arises out of the ent[illegible] of its workers for the impetus that it has provided to Tax[illegible] And like the early anatomists, some of the biosystematists a[illegible] vinced that this is Taxonomy and that there is no other ad[illegible] approach to Taxonomy. Thus, some would take unto Biosystematics the classical objectives of Taxonomy and again leave only classification and nomenclature to Taxonomy and to Systematic Botany. I think that it is now clear that Biosystematics is a valid and very important aspect of Systematic Botany as here outlined and, as such, a significant tool of Taxonomy. I[illegible], however, is on the plane of integration as well as of comparis[illegible] It utilizes Comparative Cytology and Comparative Genet[illegible] seeks to determine relative crossability and relative inter[illegible] and seeks an analysis of the genetic constitution of natural [illegible]tential interbreeding populations. It attempts to classify the genetic units of such populations in terms of the [illegible] phenomena that initiate them, the isolating mechanisms [illegible] whose sanction they develop and the nature of the environmental forces that permit their survival. To this end, it uses such terms as ecospecies, ecotypes, ecoclines and cytotypes, though this terminology is as yet a long way from being settled as to its precise role in Biosystematics. Since these same genetic and cytological phenomena are responsible for the morphological and physiological character of the individuals that make up natural populations, Biosystematics is sometimes fittingly spoken of as "studies in the nature of species" and its dynamics are often spoken of as "speciation." It approaches the ideal Taxonomy when it seeks to establish phylogenetic relationship among the members of a genus. It is our only means of establishing true genetic relationship.

This brings up the point as to the difference between phylogenetic relationship of the taxonomist, and genetic relationship as construed by the geneticist. Phylogenetic relationship is the system of genetic lineages that have brought us our species populations as they exist today. Its interpretations are drawn from the irretrievable past. It is the field of relationship that is of major concern to the taxonomist and he would like nothing more than to be able to reconstruct the pattern of genetic lineage that has been traversed. The phrase "genetic relationship" etymologically means precisely the same thing as phylogenetic relationship. As this phrase is used by geneticists, however, it means more than that. It includes also, in effect, the entire genetic potential of related species populations, the known facts of which are [illegible]t through manipulation to determine relative crossability a[illegible]e relative intersterility of progeny. It is concerned with th[illegible] total of genic materials capable of being exchanged and [illegible]hods by which this may be accomplished.

[illegible] difference is entirely comparable to the difference between [illegible] relationship and genealogy in any randomly selected [illegible] of people or between the races of man. It would require [illegible] relatively few generations of carefully supervised mating [illegible] thoroughly the gene pattern available. It would require an enormous number of generations back through time to reach a point of common genealogical origin for the individuals or the groups. Obviously such groups are more closely related genetically than they are genealogically. Similarly is it possible for certain species, subspecies or populations to be more closely related through genetic potential than they are related phylogenetically The taxonomist cannot operate in the field of potential situations. He must therefore draw a careful line between the dynamics of the past and those of the future. He can use genetic facts of the present where they shed light upon the dynamics of the past but he must leave the future to the elements [illegible]at may build natural populations under the sanction [illegible]ect[illegible]e natural environment. When these are accomplished, he [illegible] have additional material for his synthesis. A case in point is evidence indicating the close genetic but distant phylogenetic relationship of *Platanus orientalis* L. and *P. occidentalis* L. through their fertile hybrid, *P. acerifolia* Willd. Here the old and new world world parents have presumably been separated at least since Miocene time if not since Cretaceous time and have diverged [illegible]ificantly through genetic processes both morphologically and physiologically so that the taxonomist has recognized in them two species. When brought together artificially, they cross with the production of a fertile hybrid. Some geneticists and biosystematists argue that this is evidence that they should be classed as subspecies of a single species, however remote the phylogenetic ancestry. It is important here to realize that both the morphological and the physiological divergence of these two species are each the result of genetic change, resulting, presum[illegible] the accumulation of enormous numbers of successive [illegible]ns or other chromosomal changes. Somehow these did n[illegible] involve a sterility barrier, or if they did, a reverse mutation or [illegible] compensating mutation that wiped it out may have occurred later. In any event, no one has demonstrated that the progeny can or will establish themselves in a natural stand and serve as a bridge for the persistent exchange of genes between the two parents. This is an interesting case but let it be emphasized that the taxonomist cannot deal in futures. It is obvious that not all of the total genic complement involved in potential genetic situations goes into every lineage. There is no way of predicting how much or what part of the genic complement will be involved in any particular case and whether or not the resulting combination will survive environmental selection. The taxonomist can operate effectively in such cases primarily on morphological, physiological and palaeontological evidence. On this evidence these divergent populations have reached a level of differentiation which permits them to be regarded as taxonomically different and yet there is sufficient evidence of relationship such as permits them to be included in the same genus. Whether they be classed as species or subspecies will depend upon the judgment of the classifier in assessing the role of the two entities in the taxonomic system of the genus. We do not as yet know enough about the nature of sterility barriers or of retained fertility to assess them phylogenetically. We can assess them only in terms of present day genetic potential and genetic opportunity.

It is likewise possible that two entities may be more closely related phylogenetically than the degree of possible gene exchange between them would indicate. Through any of several cytogenetic mechanisms a sterility barrier may be erected isolating one population from another so that no further gene exchange between them is possible. Such a population in its inception may be only one generation removed from the other phylogenetically, yet the genetic barrier between them may be complete. When polyploidy is involved as the cytogenetic mechanism, morphological and physiological differences in the progeny sometimes are achieved that are of such magnitude as to warrant taxonomic recognition. Here, again, the taxonomist is interested not only in the taxonomic rank of the entity but also in the phylogenetic lineage involved over and above the genetic evidence derived from manipulation.

On the other hand, where natural introgression can be demonstrated, it is obvious that we are dealing with the accomplished junction of two lineages in a reticulate pattern of phylogeny. The taxonomist must consider such cases. It seems therefore important for the taxonomist, in adjudging the findings of the biosystematists, carefully to consider in each case whether it is evidence of an accomplished natural fact or of a potential situation whose unfulfilled actuality lies in the nebulous future.

It is possible to work biosystematically only with plants between which genetic manipulation is both possible and practical. This of course limits the sphere of its usefulness enormously. Its usefulness is chiefly on the subspecific level. Often, however, it yields facts that prove eminently useful to the taxonomist in formulating his species concepts. Biosystematics then furnishes another source of facts organized systematically to stand independently in their own right, or some of which may also effectively serve the taxonomist in his synthesis.

Some biosystematists prefer to speak of their field of research as experimental taxonomy. If we can assume that experimentation and manipulation are synonymous, such a term as Experimental Taxonomy might be regarded as validly applied. However, I think most workers regard the results of experiments as strictly objective since experimentation presumably establishes proof or disproof. We may establish proof of genetic relationship in the limited sphere where this is possible. If we can then demonstrate that the genetic relationship is precisely what the phylogenetic relationship has been the term Experimental Taxonomy is a valid one. In the overwhelming majority of cases, however, it is necessary to adjudge the situation in terms of our concepts of phylogeny before assigning taxonomic rank and position. In the postulation of such phylogenetic relationship, we strive toward an ideal through the exercise of judgment. It is doubtful whether judgment, apart from the facts upon which it rests, is subject to experiment. Because of this, most genetic manipulation in Taxonomy falls short of being an experiment.

Another aspect of Taxonomy is what has been termed the taxonomic system. There are many botanists who would regard the system as the ultimate goal of Taxonomy since it provides the basis of classification. There is, however, confusion of concepts evident in this point of view since classification is the basis of building the taxonomic system, rather than the taxonomic system the basis of classification. The taxonomic system may serve as a tool in identification or may serve as a tool of expression of relationship.

It is important to point out that today orders and families are placed in the system not to indicate a lineal sequence of phylogenetic relationship from order to order or from family to family. Rather, these names stand in lieu of combinations of characters, and their arrangement expresses successive modifications of characters thought to have been followed in the evolutionary history of the orders and families. The plant groups as we know them today are obviously the end points in many such phylogenetic sequences built upon a divaricate pattern. What lies before us now is a cross section of the phylogenetic lineages that have resulted in the orders and families as we know them today. How far back in the lineage a given genus or a family or an order may have diverged is now wholly conjectural. It would indeed be hazardous to assume that of two orders arranged in sequence the higher originated in the lower. The utility of the phylogenetic system rests in the fact that by knowing the characters of the orders and families, the botanist can interpret the system and can find an expression of the interrelationship that is construed to exist.

The taxonomic system involves the arrangement of plant groups in a series of hierarchical categories, which I shall refer to as the taxonomic structure. This at once introduces a dual concept as to the meaning and use of taxonomic categories. They may be spoken of in relation to the taxonomic structure, wherein they constitute an arrangement of empty abstract categories, or they may be spoken of in relation to the taxonomic system, wherein we deal with actual plants and animals organized in terms of the categories of the taxonomic structure. When we use the term "species" without reference to any group of organisms under consideration, we are speaking of the abstract category in the taxonomic structure. When we speak of the species of the genus *Pinus,* we are referring to organized entities of the taxonomic system. Because of difficulties involved in attempts at definition of taxonomic categories, it is important that this distinction be kept in mind. The categories of the taxonomic structure involve a series of inclusive groups of different value as one descends from the kingdom through phylum, class, order, family, genus, and species. The wisdom of past experience has dictated that the taxonomist purposely refrain from defining these categories in any way that will impose restrictions on the freedom with which he may express the interrelationships that he construes to exist. However, the inclusive sequence or relative position of the categories with respect to one another is important and is fixed by international agreement (Briquet, 1935). This constitutes a basis for the relative evaluation of the categories. A relationship among plants that one taxonomist may wish to express in terms of three families in one order may be regarded by another taxonomist as better expressed in terms of three separate orders. This constitutes a legitimate difference of opinion wholly consistent with the nature of the facts and with the objectives of taxonomy. The facts necessary for an objective Taxonomy are not at present available except possibly on an exceedingly limited scale. However, in order to organize our materials into a workable system, it has been necessary to bridge the gaps in our knowledge with hypotheses. For this reason, the systems of classification are largely if not wholly subjective. They constitute the working hypotheses of the taxonomist. The hypotheses, however, are not nebulous; they have been based usually upon comparative morphology interpreted in terms of current concepts of what constitutes evidence of relationship and are subject to modification as new evidence from any source may develop. The expressed relationships are mostly incapable of proof, but are subject to personal acceptance or personal rejection by taxonomists. The "empty" categories in the taxonomic structure are incapable of inclusive and exclusive definition in any way that is phylogenetically or taxonomically significant. It therefore seems evident that there can be no absolute system of classification arranged on a structure of clearly defined and precisely evaluated categories. Under these circumstances, the taxonomic structure will better serve the needs of the taxonomist if its categories remain elastic and relative. An illustrative case is presented by *Phlox gracilis* Greene of the Polemoniaceae. During its taxonomic history, it has found a place in *Phlox, Gilia, Collomia, Microsteris,* and *Navarretia.* Professor Wherry, a student of the Polemoniaceae and especially of the genus *Phlox,* sees in this species characters which he deems sufficient to exclude it from *Phlox.* Being informed also on the other genera in the family, he knows that it is not at home in any of these, so he follows the latter decision of Greene and elevates it to the category of a separate genus, *Microsteris.* So long as Professor Wherry construes evidence of relationship as he does, he is absolutely correct in his disposition of this species. I, who also am a student of the Polemoniaceae, see in this species evidence of such close relationship to *Phlox* that I believe that the objectives of taxonomy are better served by including it in *Phlox,* even though it demands subgeneric status in that genus. So long as I construe relationship as I do I am equally correct in placing it in *Phlox.* I think Professor Wherry and I understand each other in this matter. There are no definitions of the genus or of the species, as such, that compel us to unify our treatment. The important point about this example is not what happens to nomenclature and not that two experts disagree. It is rather that each of us is free to express relationships as we see and interpret them in terms of a system of classification and a nomenclature that may be judged by those botanists who may wish to use them. The resultant differences in nomenclature and synonymy serve as tools in the taxonomic system and reflect two concepts of relationship, or five concepts of relationship if we consider the entire synonymy. Taxonomy is obligated to a stable nomenclature only to the point of consistency with its objectives. When synonymies are once worked out and properly cited, nomenclature is stable to anyone who understands the objectives of taxonomy, the use of indices, and the methods of citation. This is little enough to expect of all informed botanists. To many other branches of learning, synonymy is a welcome symptom of the richness of the language. To the taxonomist, it is a tool of expression for his concepts which he hopes will not become unwieldy. The non-taxonomist, it seems, looks upon synonymy as a symptom of the *rigor mortis* of taxonomy.

There have been many attempts by taxonomists and others to define the categories of the taxonomic structure. Many of these attempts rest on an assumption that the category possesses objective reality. And most of these have attempted to define the species category. Their authors, unfortunately, have largely confused concepts involved in definition with concepts involved in characterization as well as concepts of phylogenetic relationship as construed by the taxonomist with those of genetic relationship as construed by the geneticist. The concept of definition involves the circumscription of limits; a definition must be both inclusive and exclusive. I have seen no putative definition of a taxonomic category so worded as to be incapable of application either to the next higher or the next lower category of the taxonomic structure. That which is a species to one taxonomist may be a subspecies to another, and that which is a family to one may be an order to another. This difference of opinion is wholly consistent with the nature of the known facts and does no harm to the objectives of Taxonomy. The empty category of the taxonomic structure has no foundation in reality and obviously cannot be objectively defined. If the category in the taxonomic system has reality, it may be defined only in terms of the particular plants comprising it. It is my personal belief that there is no significant definition possible that can be applied categorically in the taxonomic structure or in the taxonomic system to the total exclusion of the next higher or the next lower category. Taxonomic categories possess only relative values insofar as we are now in a position to understand them. Until they can be made objective, it is best that they remain relative and elastic in their application. The sphere of relativity is solely with respect to the next higher and the next lower category within the immediate sphere of taxonomic relationship. An interpretation as to what constitutes a species of pine has little meaning relative to an interpretation as to what constitutes a species of *Rosa* even though the specific category is used for both. However, within the genus *Pinus* one is more nearly able to develop concepts of comparative evaluation without at the same time being able to fix these values at their precise level in the taxonomic structure to the satisfaction of all. In such a sphere of relationship, it is strictly within the province of sound logic and observable fact for a taxonomist to hold concepts of species which may cause him to be regarded as a "splitter" with one segment of a group and a "lumper" with another. At its worst, lumping is the tool of the superficial and splitting the tool of the uncritical. There are, however, depending upon the nature of the problem, intelligent uses for each procedure that are both necessary and desirable. In most cases, relationship can be expressed only in terms of relative nearness of relationship, and within the plant kingdom all degrees of relationship exist. This situation can be reduced to a system of rigidly defined categories only by arbitrary decisions which result in artificial categories. *Pinus radiata* is a species of a relatively large genus. Because of certain common characteristics which are construed to indicate relationship, this and other pines are aggregated into the genus *Pinus*. *Pinus* differs in several characters from *Abies* and *Tsuga,* but because of certain other common characters, these three genera, along with several others, are aggregated into the family Pinaceae. In a like manner, Pinaceae, Taxodiaceae, and Cupressaceae differ from one another but are grouped with other families under the order Coniferales. Thus the species *Pinus radiata* is only a small part of the genus *Pinus*, the family Pinaceae, and the order Coniferales. *Ginkgo biloba*, on the other hand, is not only the only living species, but is also the living genus, the family, and the order. Whereas, in *Pinus radiata*, we can enumerate characters that indicate in turn the species, the genus, the family, and the order, in *Ginkgo biloba* there are no characters of structure or function significant to any conceivable definition of these taxonomic categories that can be utilized to designate each in turn in the living member. The position of *Ginkgo biloba* in the taxonomic system is significant only as an order in the class Gymnospermae and coordinate with the orders Coniferales, Taxales, and Cycadales. In this case, there is no foundation for evaluation in definitive terms in any of the categories below the order. Obviously, the living *Ginkgo biloba*, the species, is precisely the same genetically as the living *Ginkgo*, the genus, Ginkgoaceae, the family, and Ginkgoales, the order. There is no way of defining the species on a genetic basis in this case that will exclude the genus, the family, or the order, without setting up some arbitrary criteria. A concept of species is significant only in a genus of more than one entity. I cite these cases to point out that taxonomic categories are relative and that the sphere of relativity rests among the species of a genus, the genera of a family, and the families of an order. It rests in closeness of relationship and not across the entire taxonomic structure.

Taxonomy is one of the few sciences that documents its results by preservation of actual plant materials that have served as a basis for its concepts. Through the citation of specimen vouchers and their permanent preservation in herbaria, the literature of Taxonomy is forever current and always in demand. The Species Plantarum (1753) of Linnaeaus is in continued demand through its documentation in the specimens preserved in the Linnaean herbarium, however archaic the system of classificaiton may be that was utilized in it. Were it not for the Linnaean herbarium, the Species Plantarum and its nomenclature would long since have passed to the limbo of literary novelties, much as the ancient herbals, and serve only to tantalize the student as to what the author might possibly have had in mind when he described, imperfectly or incompletely, this or that species of plant. It could not possibly have been utilized as the boundary of priority of nomenclature. Similar documentation of the results of research should be urged upon the other divisions of botany.

Taxonomy can only bring itself up to date. It cannot advance independently of the basic disciplines upon which it rests. It is important to all of the basic disciplines, however, that Taxonomy keep itself up to date with the state of development of each of them. Knowledge of the interrelationships of plants is the key to many problems that arise in botany, the applied sciences, industry, and agriculture. One discouragement the taxonomist has had to face throughout this past century is that although systematic morphology clearly provided the basis for Taxonomy and the foundation for the natural system and pointed clearly through the theory of evolution to the phylogenetic systems, detailed advances in Morphology and Anatomy beyond this point were for a long time largely inadequate to help him solve his problems. The Morphology upon which classical Taxonomy rests is little more than simple organography involving position and number of parts, adhesion, cohesion, abortion, and modification of floral organs. This method has centered around the concept of Wolff (Samassa, 1896), championed by Goethe (1790) that the flower was a modified shoot and that its organs were homologous with leaves. It has accepted in its phylogenetic approach DeCandolle's idea that in the natural system anything which tended to obscure basic symmetry was a mark of advance in the system. The fact of the matter is that we are not as yet agreed as to what a flower is in terms of its homologies. We are in almost complete ignorance of the phylogenetic sequences in the development of the parts of the flower. There is much disagreement among morphologists and anatomists as to the meaning of vasculation in these organs in terms of arriving at homologies. These and many other unsolved problems of systematic morphology are vital to a sound phylogenetic Taxonomy. Research in Taxonomy has largely skirted these problems, with the result that there has been no sound advance in this aspect of the science. Instead, research in Taxonomy has centered chiefly in organizing the genus and species and ordering the nomenclature.

If Taxonomy is to fulfill its function in the botanical sciences, it must shift its emphasis from purely organizational techniques to include active research in some of the basic disciplines upon which Taxonomy rests. The taxonomist can be of little service to the objectives of his science by the pursuit of organizational monographs executed without contemplation of the basic problems upon which the science rests. The taxonomist must become a morphologist, a cytologist, a geneticist, and we hope, in time also a physiologist, and a biochemist. There is no field of specialization in taxonomy apart from these disciplines that is in any way adequate to the problems that confront the taxonomist. It makes little difference what area of the taxonomic structure or the taxonomic system he is investigating, because, with the exception of the riddles of nomenclature, the problems upon which he passes judgment are all basic botanical problems. In the higher categories, his problems thus far have been concerned chiefly with the evaluation of the structures of the flower as he seeks evidence concerning phylogenetic sequence of its structures. Some new lines of approach are now available from the field of Anatomy. In order that his judgment may be sound, he must master the research techniques of Comparative Morphology and Comparative Anatomy and Histology and apply them to his problem. He must be in a position to judge for himself the controversial matter in these fields as it applies to his problems. If his researches are on the level of species and genera, he must, in addition, master the research techniques of the cytologist and the geneticist, so that he may utilize the tools developed in these sciences for the interpretation and evaluation of variation and intergradation. It is only from these points of view that he will be able to assess his problems in terms of the expression of the interrelationships that are his objectives. The taxonomist must first of all be a botanist with the broadest of training. Only then will he be capable of being a competent taxonomist.

SUMMARY

In the various works dealing with the general field of Taxonomy, we may arrive at many different concepts as to the meaning of the terms "Taxonomy" and "Systematic Botany." Most definitions, however, have regarded the two terms as synonymous even though usage in the same work differed sharply from the definition stated. Since there is need for a term applicable in the sense in which Solereder used Systematic Anatomy, and since little is to be gained by invoking a new term, it now seems necessary to make an arbitrary choice between these definitions and usages.

Through usage, over and above definition, De Candolle supplied the classical Taxonomy with a method and an objective that served to establish the term "Taxonomy" in the inclusive sense we here advocate. His usage involved the methodology and tools concerned with taxonomic research, classification, nomenclature, the taxonomic system and the determination of relationship. Since De Candolle, we have added little to the classical concept of taxonomy except additional and improved method and additional botanical fact. The objective remains the same, namely the classification of plants into a system that expresses their interrelationships. All that the theory of evolution accomplished immediately for taxonomy was to make clear the meaning of the selfsame "relationships" that De Candolle sought, namely the relationship based upon resemblance or community of characters which now becomes the evidence of relationship through common evolutionary descent. Being first associated with the natural systems, the term "Taxonomy" was at its inception inescapably linked with the motive of establishing relationship among plants.

With the adoption of this broad concept of Taxonomy as herein advocated, there is no need today for the term "Systematic Botany" used in a sense that is synonymous with Taxonomy. There is, however, an important use for the term "Systematic Botany." This is its application to the systematic approach to any of the basic divisions of Botany, much as Solereder used the

term "Systematic Anatomy." Its objective will be the establishment of botanical facts upon which concepts of relationship are based rather than simply the establishment of relationship. This is the field of botanical research upon which Taxonomy rests.

With such a concept of Taxonomy and Systematic Botany, Biosystematics fits naturally into Systematic Botany on the plane of integration. It seeks to establish facts about a systematic group in systematic order so that these may be used in the synthesis of taxonomic relationships.

Department of Botany,
University of California, Berkeley

Literature Cited

Benson, L. 1943. The goal and methods of systematic botany. Cactus and Succulent Jour. 15: 99–111.

Bremekamp, C. E. B. 1939. Phylogenetic interpretations and genetic concepts in Taxonomy. Chron. Bot. 5: 398–403.

Briquet, J. 1935. International rules of botanical nomenclature. Jena.

Camp, W. H. and C. L. Gilly. 1943. The structure and the origin of species. Brittonia 4: 323–385.

Candolle, A. P. de. 1813. Theorie elementaire de là botanique. Paris.

Clausen, J., D. D. Keck, and Wm. M. Heisey. 1940. Experimental studies on the nature of species. I. Effect of varied environments on western North American plants. Carnegie Inst. Wash. Publ. 520.

————. 1939. The concept of species based upon experiment. Am. Jour. Bot. 26: 103–106.

Dobzhansky, T. 1941. Genetics and the origin of species. 2nd revised edition. New York.

Engler, A., and E. Gilg. 1924. Syllabus der Pflanzenfamilien. Berlin.

Gilmour, J. S. L. and W. B. Turrill. 1941. The aim and scope of taxonomy. Chronica Bot. 6: 217–219.

Goethe, J. W. 1790. Versuch die Metamorphose der Pflanzen zu erklaeren. Gotha.

Hall, H. M. and F. E. Clements. 1923. The phylogenetic method in taxonomy. Carnegie Inst. Wash. Publ. No. 326.

Le Maout, E. and J. Descaisne. 1876. A general system of botany. Translated by Mrs. Hooker. London.

Lindley, J. 1830. An outline of the first principles of botany. London, Longman.

————. 1853. The vegetable kingdom. London.

Linnaeus, C. 1753. Species plantarum. Holmiae.

Mayr, E. 1942. Systematics and the origin of species from the viewpoint of a zoologist. New York.

Radlkofer, L. 1883. Über die methoden in der botanischen systematik, insbesondere die anatomische methode. Festre de zur vorfeier des allerhöchsten geburts-und namenfestes Seiner Majestät des königs Ludwig II gehalten in der K. Akademie der wissenschaften zu München am 25 juli 1883. München am Verlage der K. B. Akademie, 1883.

Samassa, Paul. 1896. Caspar Friedrich Wolff's Theoria Generationis. Leipzig.

Solereder, H. 1899. Systematische anatomie der dicotyledonen. Stuttgart.

Turrill, W. B. 1942. Phylogeny and taxonomy. Bot. Rev. 8: 247–270; 473–532; 655–707.

Wettstein, R. 1924. Handbuch der systematischen botanik. Leipzig.

POLYPLOIDY IN ECHINOCYSTIS

Thomas W. Whitaker

During the course of a survey of wild and cultivated species of the Cucurbitaceae to determine the host range of the cantaloupe mosaic virus, I have had an opportunity to study at first hand living material of a great many species of this interesting and diverse family. In conjunction with the mosaic studies, cytological investigations were initiated, and a technique was developed to study the chromosomes by modern methods. As an incidental part of the latter investigation, I had occasion to examine *Echinocystis macrocarpa* Greene, the chilicothe or mock-cucumber native to coastal California from Monterey Bay southward to Lower California, Mexico.

McKay (1931) studied *Echinocystis macrocarpa* and two other West Coast species (*E. fabacea* Naud. and *E. oregana* Cogn.) and reported that each species has 16 pairs of chromosomes. *Echinocystis lobata* T. & G., a species of the eastern United States, is apparently a diploid, since it was reported by Kirkwood (1907) to have sixteen pairs of chromosomes.

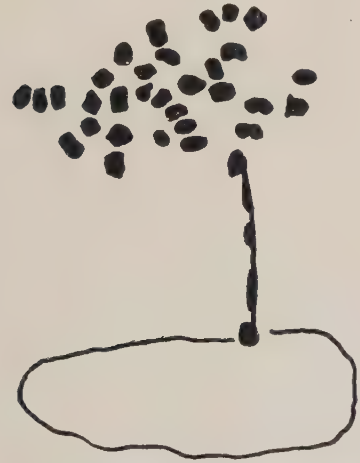


Fig. 1. *Echinocystis macrocarpa:* late anaphase showing 32 chromosomes; note chromatin bridge. Lower grouping shown only in outline. ×2400.

Plants of *Echinocystis macrocarpa* that I have sampled in San Diego County, California, have thirty-two gametic chromosomes (fig. 1). Evidently, they are tetraploid. Meiosis is characterized by an occasional multivalent and chromosome bridge; otherwise, the meiotic divisions are perfectly normal. In lactophenol the stainable pollen averages about 97 per cent. These observations argue against the possibility of this material of *E. macrocarpa* being a recent autopolyploid. Specimens on which these counts are based have been deposited in the Herbarium of the University of California, Berkeley, California.

There is some supporting evidence from morphological characters for the tetraploid nature of *Echinocystis macrocarpa*. The fruits and seeds in particular exhibit "gigas" characters. The fruits are normally three to six inches long and two to three inches in diameter, considerably larger than the fruits of other species of *Echinocystis* in the Pacific Coast area. The contrast in seed size is not so great as that found in the fruit; nevertheless, the average size of seed is apt to be larger in this species.

The discovery of a naturally occurring, numerical polyploid in the Cucurbitaceae is of unusual significance. Numerical polyploids are exceptionally rare in this family and have been found in only one other genus, *Trichosanthes,* although fifteen or more genera have been studied cytologically. Nakajima (1937) reports that the dioecious species *T. cucumeriodes* Maxim. has twenty-two pairs of chromosomes, whereas *T. japonica,* also dioecious, has only eleven pairs.

The above facts suggest that evolution at the species level in the Cucurbitaceae has proceeded for the most part by genic differentiation. For example, in the relatively large and greatly diversified genus *Cucurbita,* evidence from species crosses (Whitaker, unpublished) indicates that the difference between some of the species is dependent upon a comparatively small number of single gene mutations. Thus, it seems safe to conclude that evolution in this large and diverse family has proceeded mostly by genic differentiation (at the species level), supplemented by the infrequent occurrence of polyploidy.

Bhaduri and Bose (1947) have interpreted their observations to mean that increase in chromosome number in this family is primarily due to allopolyploidy, combined with fragmentation of chromosomes at particular loci. Their evidence is largely indirect, and, in any event, does not provide a critical test for their assumptions. However, these suggestions are stimulating and subject to experimental attack. By the use of colchicine and modern cytological methods, it should be possible to obtain some insight into the question of fragmentation. The most favorable genus for this work would undoubtedly be *Cucumis,* where *C. sativa,* the cucumber, has seven pairs of chromosomes, and the remaining species are reported to have eleven and twelve pairs.

To summarize, the discovery of a natural, numerical polyploid in the Cucurbitaceae is of some biological significance for several reasons. First, it indicates that polyploidy may have had an important role in the evolutionary development of certain genera in the family. Second, it tends to harmonize the evolutionary pattern in the Cucurbitaceae with that found in other dicotyledonous families.

Bureau of Plant Industry, Soils and
Agricultural Engineering,
Agricultural Research Administration,
United States Department of Agriculture,
La Jolla, California.

LITERATURE CITED

BHADURI, P. N., and P. C. BOSE, 1947. Cytogenetical investigations in some common cucurbits, with special reference to fragmentation as a physical basis of speciation. Jour. Genetics 48: 237–256.

Kirkwood, J. E. 1907. Some features of pollen formation in the Cucurbitaceae. Bull. Torrey Bot. Club 34: 221–242.
McKay, J. W. 1931. Chromosome studies in the Cucurbitaceae. Univ. Calif. Publ. Bot. 16: 339–350.
Nakajima, G. 1937. Cytological studies in some dioecious plants. Cytologia, Fujii Jub. Vol. 282–292.

IRA WADDELL CLOKEY

The death of Ira Waddell Clokey at his home in South Pasadena, California, on January 13, 1950, marks the passing of a man whose career was extraordinarily useful to the science of botany even though botany was but an avocation with him. Born at Decatur, Illinois, on December 21, 1878, Ira Clokey was the son of Josiah Mitchell Clokey and Susan Carrie Elson. He attended the University of Illinois and Harvard University, receiving from the latter in 1903 the degree of Bachelor of Science *cum laude* with a major in mining engineering, a profession which he followed until 1920, when he entered Iowa State University to specialize in botany. He received the degree of Master of Science in Plant Pathology from this institution in 1921.

As a boy, Ira Clokey showed an avid interest in botany and this interest remained with him as long as he lived. In Decatur High School, one of his classmates was H. A. Gleason, and together they went on many a trip to collect and study the flora of Illinois. His career as a mining engineer took him in 1904 to Mexico, where he remained for seven years, and in 1915 to Colorado. In both regions he collected extensively, and built up a herbarium containing an excellent representation of the plants of each area. Unfortunately, in 1912, his herbarium, containing all of his Mexican collections and some of his early Illinois material was destroyed by fire. The fact that the duplicates of his Mexican collections had never been distributed, is a great loss to science. His later collecting was pursued with a view to rebuilding his herbarium through exchange. With this end in mind, he collected many duplicates, and as a result, there are few herbaria in the world that do not have representatives of his collections. Despite his having collected in large quantities, his specimens were beautifully prepared.

Mr. Clokey's early interest in botany centered around the genus *Carex* and he carried on extensive correspondence and exchange with several of the caricologists of the early part of the current century. As a result of these early exchanges, much of the classical material of the genus *Carex* is in his herbarium.

In 1935 Mr. Clokey became interested in the flora of the mountains of the southwestern United States and selected the Charleston Mountains of southern Nevada for intensive study. Here he collected large sets and it may be said that through his efforts, the flora of the Charleston Mountains in Nevada is perhaps more completely represented in major herbaria than is the flora of any equal area of the world. Through the cooperation of the Civilian Conservation Corps, many of these specimens were collected in sets of 100 to 150. All of these were distributed, some of them as Gray Herbarium Exsiccatae No. VIII. His intensive field work in the Charleston Mountains covered a period of approximately seven years. To work up this material, Mr. Clokey enlisted the aid of many specialists who treated the families and genera of their special interest, but as may be noted in the appended bibliography, he himself published several papers treating special groups in this area. The manuscript for the "Flora of the Charleston Mountains" was completed and accepted for publication by the University of California Press just prior to Mr. Clokey's death.

As recreation from his studies on the Charleston Mountain flora, Mr. Clokey engaged in researches on the genetics of maize, the work being carried on largely in collaboration with Dr. E. G. Anderson of the California Institute of Technology. This seeming divergence may be accounted for by the fact that while he was at Iowa State University he had developed considerable interest in the field of genetics under the influence of the late E. W. Lindstrom.

No one as whole-heartedly interested in botany as was Ira Clokey could have been satisfied without building up a sizeable botanical library. He expended considerable time and energy in obtaining complete sets of botanical journals and was jubilant when a missing number was finally acquired and the series in question thus made complete. In addition to the journals and many miscellaneous and indispensable references, his library contained the majority of the floras treating various parts of the United States. The California Institute of Technology at Pasadena is indeed fortunate in having this collection presented to it as the Ira W. Clokey Memorial Library.

In 1941, Mr. and Mrs. Clokey deposited the Clokey Herbarium at the Universiy of California with the understanding that it become the property of the University at Mr. Clokey's death. From that time until the present, most of the Clokey Herbarium exchange has been carried on through the Herbarium of the University of California. Containing an estimated 102,600 specimens, the Clokey Herbarium constitutes the largest single collection ever received by the Herbarium of the University of California. It exceeds in size the Brandegee Herbarium which might be said to be the nucleus of the University of California herbarium.

To Mr. Clokey, botany was always a source of happiness which he pursued with vigor. He was a cheerful, intense man with a keen sense of humor. I shall never forget his amusement

PLATE 13. IRA WADDELL CLOKEY.

over having sent fourteen specimens of a very complex species to a specialist and having them returned to him under fifteen different names. I believe he doubtfully accepted three entities as involving the fifteen names. He retold this story many times, always closing it with rollicking laughter.

Mr. Clokey is survived by his widow, Mrs. Cleora Brooks Clokey, who accompanied him on many of his collecting expeditions and who often assisted him with the preparation of specimens, and by two daughters.—Herbert L. Mason, Department of Botany, University of California, Berkeley.

Bibliography of I. W. Clokey's Botanical Publications

1916. A new hybrid Carex from the middle western states. Torreya 16: 219–220.
1919. Carex notes. Rhodora 21: 83–85.
1922. Carex notes. Carex apoda sp. nov. Am. Jour. Sci. 3: 88–91. 1 plate.
1931. Notes on the flora of Santa Cruz Islands, California. Bull. So. Calif. Acad. Sci. 30: 60–61.
1934. (and E. G. Anderson) Chromosomes involved in a series of interchanges in maize. Am. Midland Nat. 68: 440–445.
1937. A new Penstemon from the Charleston Mountains, Nevada. Madroño 4: 128–130. [Notes on the flora of the Charleston Mountains, Clark County, Nevada. I.]
1938. Notes on the flora of the Charleston Mountains, Clark County, Nevada. [II.] Bull. So. Calif. Acad. Sci. 37: 1–11. 2 plates.
1939. Notes on the flora of the Charleston Mountains, Clark County, Nevada. III. Bull. So. Calif. Acad. Sci. 38: 1–7.
1939. (and D. D. Keck) Reconsideration of certain members of Penstemon subsection Spectabiles. Bull. So. Calif. Acad. Sci. 38: 8–13.
1942. Notes on the flora of the Charleston Mountains, Clark County, Nevada. IV. Astragalus. Madroño 6: 211–222. 1 plate.
1943. Notes on the flora of the Charleston Mountains, Clark County, Nevada. V. Cactaceae. Madroño 7: 67–76. 2 plates.
1945. Notes on the flora of the Charleston Mountains, Clark County, Nevada. VI. Madroño 8: 56–61.
——. In press. Flora of the Charleston Mountains, Nevada.

A GRAPHIC REPRESENTATION OF BESSEY'S TAXONOMIC SYSTEM

R. Lucas Rodriguez C.

The present diagram (fig. 1) is an effort to show Bessey's (1915) orders of Angiosperms and their relationships, with reference to the main characteristics which distinguish them and which are held to indicate their degree of primitiveness or advancement.

Studying Bessey's system one comes into acquaintance with his chart (fig. 2) in which he showed the relationship of the orders and, approximately, the number of species in each. When lines are drawn on this familiar "cactus plant" diagram to separate one characteristic from its opposite, they interweave, necessarily, in irregular fashion.

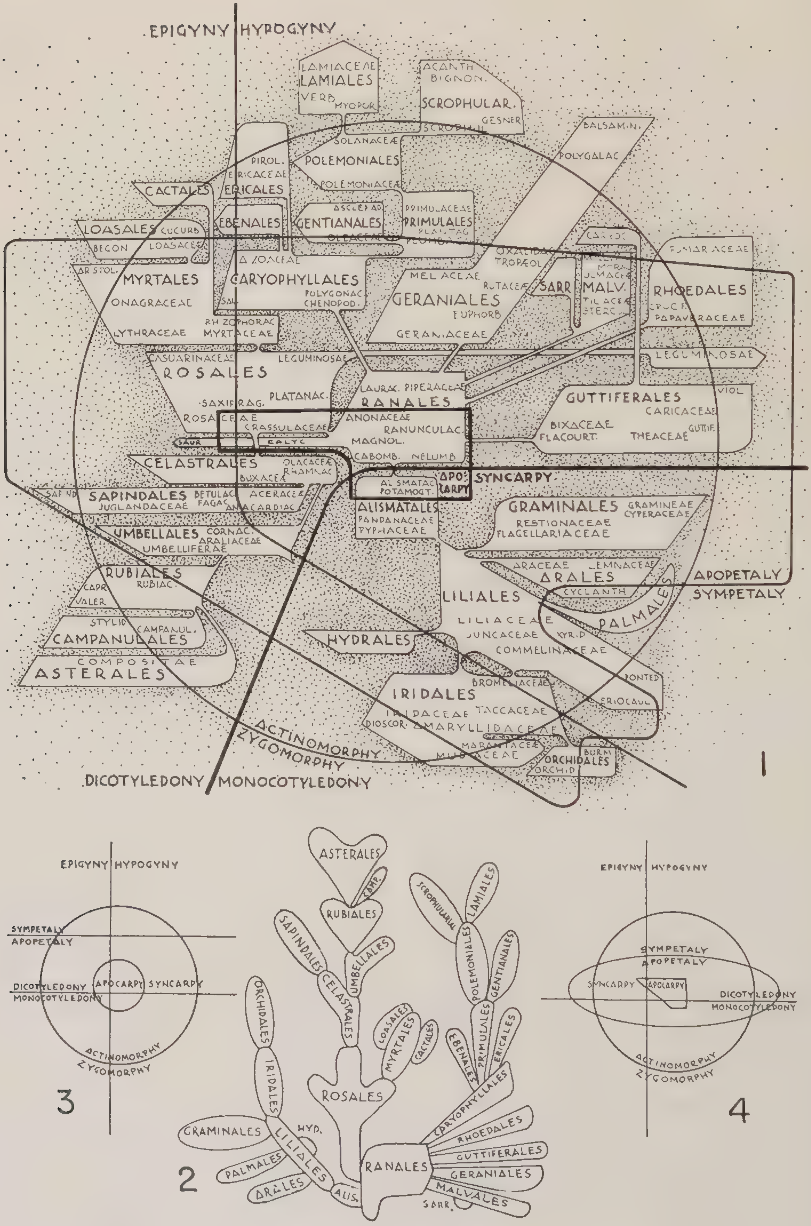
An attempt was made to plot the main divisions of characteristics significant in phylogenetic taxonomy as either straight lines or simple geometric curves (fig. 3), and make the branches of the "cactus plant" adapt to them. In this arrangement, the lines separating monocotyledony from dicotyledony, and sympetaly from apopetaly crossed at right angles that which represented the transition from hypogyny to epigyny; the transitions from apocarpy to syncarpy, and from actinomorphy to zygomorphy, were drawn as concentric circles, as required by successive levels of advancement reached by practically all postulated lines of descent. When Bessey's orders were arranged on this frame, th two most primitive orders, Ranales and Alismatales, occupied the center, and the different groups flowed radially out, the distance from the center becoming an indication of their degree of advancement. It was evident, however, that the transition to sympetaly should also be represented as a closed line, cutting in and out of the circle showing zygomorphy (fig. 4).

This layout proved more satisfactory as a starting point; but to avoid having both branches of the Oppositifoliae-Cotyloideae—the series ending in Loasales and Cactales, and that leading to the Asterales—twining around each other, it was again necessary to modify the general frame, reducing the space given to the monocotyledons and bending the line marking the change to epigyny. Such is the arrangement finally adopted for the diagram in fig. 1.

In this representation, Bessey's idea of showing the relative number of species in each group was abandoned, as the area covered by an order depends on the extremes of variation included within that order. In the diagram as given here, some families have been indicated in each order, to clarify somewhat the extension given to it.

Using this diagram as a working tool, it seemed interesting in the preparation of some seminar reports to plot additional characteristics on it, in order to compare other criteria for primitiveness with the accepted Besseyan concepts. In general, the lines marking off the trilacunar condition of the node (Sinnott, 1914) stipulate leaves (Sinnott and Bailey, 1914) and presence of endosperm, formed also closed curves, of necessity irregular but centering also on the Ranales. In each case there was at least one "avenue" along which the theoretically advanced condition reached the apparently primitive orders. The relative position of the families within each order as shown in fig. 1 already reflects the distinctions established by the additional criteria mentioned.

Bessey's original diagram has one disadvantage, that of appearing to be simultaneously a systematic chart and a genealogical tree. When the present diagram form is used, it becomes easier to keep in mind, or to show students, that neither of them is a "family tree" but a cross section at one time level (the present)



Figs. 1–4. Two interpretations of Bessey's orders of Angiosperms.

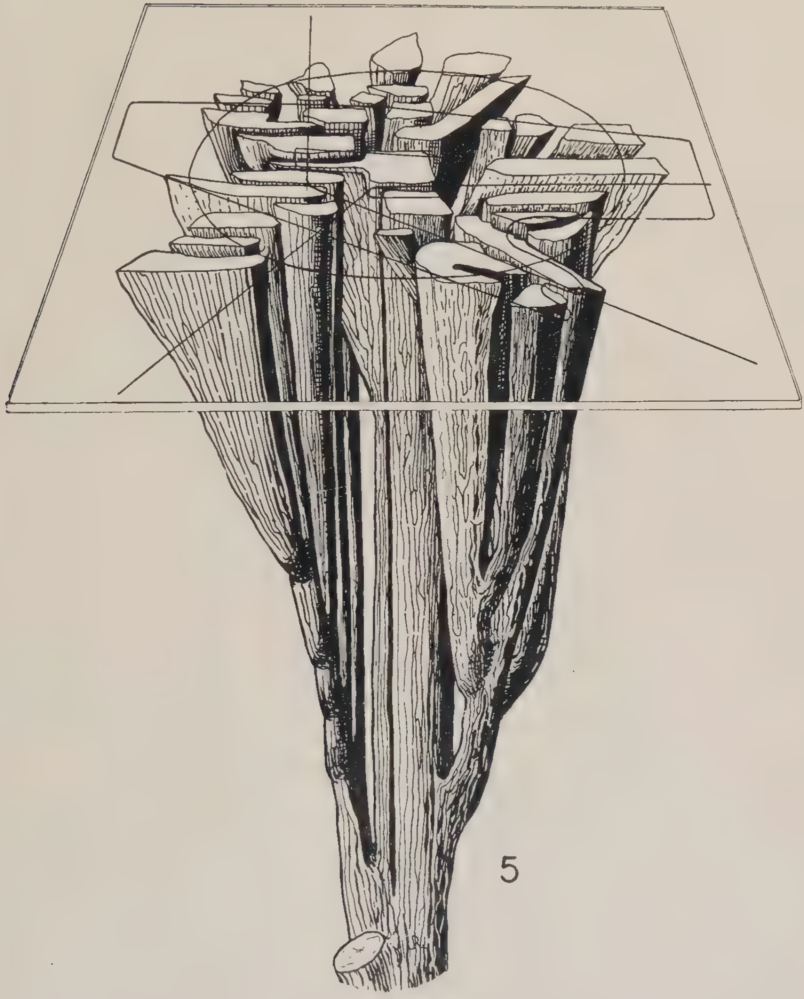


Fig. 5. The diagramatic interpretation of Bessey's system as a cross-section of the Angiosperm genealogical tree. The vertical dimension represents time. No factual value is attached to the relative levels at which the groups branch out from their putative predecessors.

of the true genealogical tree growing out of the past (fig. 5). The degree of divergence from the primitive condition corresponds to the distance from the axis of the tree, while the connections in both diagrams (figs. 1 and 2) between one order and another are projections of a connection which existed at an earlier time level. The frame of the diagram, drawn on the plane of a particular time level, is only an attempt to define the lines along which the several series are diverging from the central stock, and the order in which the different changes are achieved. Considered in this manner, the diagram comes a little closer to Lam's (1936) ideal phylogenetic model, in which each detail, dimension or direction should have a definite meaning.

Department of Botany
University of California, Berkeley

Literature Cited

Bessey, C. E. 1915. The Phylogenetic Taxonomy of Flowering Plants. Ann. Mo. Bot. Gard. 2: 109–164.

Lam, H. J. 1936. Phylogenetic Symbols, Past and Present. Acta Biotheoretica, A, 2: 153–194.

Sinnott, E. W. 1914. Investigations on the Phylogeny of Angiosperms. 1. The Anatomy of the Node as an Aid in the Classification of Angiosperms. Am. Jour. Bot. 1: 303–322.

Sinnott, E. W. and I. W. Bailey. 1914. Investigations on the Phylogeny of Angiosperms. 3. Nodal Anatomy and the Morphology of Stipules. Am. Jour. Bot. 1: 441–453.

DIOECIOUS MELANDRIUM IN WESTERN NORTH AMERICA

H. G. Baker

A history of the spread of *Melandrium dioicum* (L.) emend. Coss. and Germ. and *M. album* (Mill.) Garcke following their introduction (with impure clover seed from Europe and in rubbish from grain ships) into eastern North America has been given elsewhere (Baker, 1945, 1948a). A gradual spread westward is indicated, both species becoming more and more common in meadows, fields and waste places and along railroads in the ballast. There is no North American record of either species from a natural habitat, a fact of particular importance in the case of *M. dioicum* which seems ill-adapted for life as a weed (Baker, 1948b). In Europe plants with coloured petals occurring in cultivated land are of hybrid ancestry (involving *M. album*).

The means of introduction renders it likely that the material of "*M. dioicum*" arriving in America was already hybridised and, with the thrusting of the two obligatorily outbreeding forms into similar habitats, further hybridisation must have been an unavoidable consequence. Forms least resembling *M. dioicum* as it is known in Europe may be expected to have been selected. For this reason, now that the campions have become distributed throughout the United States, one would not expect recognisable *M. dioicum* to be found among the weeds of western North America.

The only specimens of "*M. dioicum*" from western North America available in wartime Britain were both collected in

British Columbia (woods just above sea level, Garrow Bay, Vancouver, 28 April 1935, *Whiting and Stewart,* K). They represent a shade form with rounded leaves but their calyces are very reminiscent of those of *M. album.* It was tentatively suggested (Baker, 1945, 1948a) that these plants might represent extreme segregants from the hybrid swarm occupying a habitat similar to that of one of the European parents.

I am indebted to Dr. E. P. Killip and Mr. C. V. Morton of the Smithsonian Institution, Washington, D. C., for the information that there is no specimen of *M. dioicum* from any of the Pacific States in the National Herbarium.

It was the fortunate experience of the author to accompany Drs. Jens Clausen, William Hiesey and Paul Grun on a journey from the laboratories of the Division of Plant Biology of the Carnegie Institution of Washington at Stanford, California, through Oregon and Washington to British Columbia in May and June, 1949. During this excursion it was possible to make observations upon the occurrence of *M. dioicum* and *M. album* in this region and to consult herbarium material.

A collection believed to be the first record of *Melandrium dioicum* naturalised in Western United States was made in Oregon (ca. one mile east of Vista Point, Columbia River Gorge, Multnomah County, 2 June 1949, *Baker 433,* Herbarium of Leeds University). The plants were well established beneath a canopy of softwood and hardwood trees (e.g. *Acer macrophyllum, A. circinatum, Alnus rhombifolia, Cornus Nuttallii, Pseudotsuga taxifolia* and *Thuja plicata*) near the roadside amidst a great profusion of herbaceous species and appeared to be reproducing freely by seed. The appearance of the specimens collected indicates little influence of *M. album* in the genotype and one is not given the impression that a woodland type has segregated from a hybrid swarm involving both species but rather of the establishment of *M. dioicum* by separate introduction.

The suspicion was strengthened by the observation of populations of *M. dioicum* in Stanley Park, Vancouver, British Columbia and in West and North Vancouver. In this area, this species appears to be not uncommon in wooded areas, being found both in clearings and wood borders on one hand and in dense shade on the other. Although a number of calyx characters suggests the influence of *M. album,* the general appearance of the populations as a whole suggests that their origin is to be found in a separate introduction from rather impure European stocks of the species rather than by segregation from a campion population which has pushed its way across the continent from eastern North America. In one case, the species was noticed among debris thrown from a house garden in West Vancouver and its original introduction as an ornamental plant seems likely in contrast to the manner in which pink-petalled plants became established in eastern North America.

In this connection, it may be of interest to record that *Geranium Robertianum* found growing in Stanley Park was definitely unlike that which is native to eastern North America and closely resembled European woodland material (Baker, 1949). The considerable connection between maritime British Columbia and the British Isles (until recent decades possibly closer than between western and eastern Canada), may indicate the probable source of *Melandrium dioicum* in the Vancouver area.

At the same time it is significant that Robbins, Bellue and Ball (1941) record that plants with rose-coloured petals occur in populations of *M. album* in California. These rare plants are indicators of past hybridisation with *M. dioicum* which cannot have occurred locally. The colonisation of western North America by *M. album,* although probably reinforced by introduction through the Pacific Coast ports, cannot be separated from the westward march of the white campion across North America for there are records of its occurrence from a complete chain of states from the eastern to the western coasts.

Although it is not claimed that these are necessarily the earliest records, herbarium specimens of *M. album* with the following dates have been seen from western North America. Abbreviations of names of herbaria are according to Lanjouw (1939).

California. Hoopa Valley, Humboldt County, 1901, *Mrs. M. H. Manning,* as *Silene Hookeri* (UC). Oregon, Sandy shore of North Santiam River, North Santiam Station, Marion County, 1919, *J. C. Nelson,* as *Lychnis alba* (WTC). Washington. Near Coupeville, Whidby Island, 1897, *N. L. Gardner 43,* as "Silene" (WTC). British Columbia. Coldstream Ranch near Vancouver, 1917, *Miss E. M. Warren* (K). Alaska. Sandy beach formation. Cape Nome Roadhouse 14 miles east of Nome, 1937, *C. W. Thornton* (K). Montana. Waste places, altitude 3200 feet, near Missoula, Missoula County, 1921, *J. E. Kirkwood 1103* (UC); Lake MacDonald, Glacier National Park, 1921, Mrs. *Susan D. McKelvey* (K). IDAHO. Roadside south of Moscow, Latah County, in *Agropyron* prairie zone, 1937, *R. F. Daubenmire 37490* (WTC).

It was apparent in the study of herbarium specimens that there is considerable confusion between *Melandrium album* and *Silene noctiflora* L. Table 1 shows the more obvious points of distinction for herbarium specimens.

Investigation of the phylogenetic connection between these two very similar species might lead to valuable conclusions regarding the relationship of *Silene, Melandrium* and *Lychnis,* between which genera there is considerable inter-fertility. In fact,

Table 1

Melandrium album	*Silene noctiflora*
Dioecious	Hermaphrodite
Calyx nerves without obvious anastomoses; parts without nerves greenish.	Calyx nerves anastomosing prominently; parts without nerves whitish.
Capsule with 10 teeth which stand upright or spread slightly outwards.	Capsule with 6 slightly recurved teeth.
Seeds tawny; surface bluntly tuberculate.	Seeds grey-brown; surface granulate.
Glandular hairs fairly frequent in region of inflorescence.	Glandular hairs very numerous causing marked viscidity.

a consideration of the many characters by which *Melandrium album* differs from *M. dioicum* leads to the surprising revelation that almost every one may be supplied by *Silene noctiflora!* Over one hundred years ago, Gärtner (1849) crossed *Melandrium dioicum* with *Silene noctiflora* and obtained a hybrid in which rather less than a quarter of the capsules contained up to fourteen seeds. The repetition of this cross is, therefore, of very considerable importance and a determined effort to extract a form similar to *M. album* from the products of recombination might well be successful. The evidence from geographic distribution is in harmony with such a suggestion for *Silene noctiflora* is probably of South European origin and it has been shown (Baker, 1945, 1948a) that the centre of distribution of *M. album* is in the Mediterranean region. Also, such an investigation might, once and for all, settle the arguments whether *M. album* and *M. dioicum* are to be considered specifically or merely sub-specifically distinct.

Department of Botany,
University of Leeds, England.

Literature Cited

Baker, H. G. 1945. The autecology of Melandrium dioicum (L. emend.) Simonkai, M. album (Mill.) Garcke (Lychnis) and their hybrid. Ph.D. Thesis, University of London.

————. 1948a. Studies in invasion and replacement, illustrated by species of Melandrium. Jour. Ecol. 36: 96–119.

————. 1948b. The ecotypes of Melandrium dioicum (L. emend.) Coss. and Germ. New Phytol. 47: 131–145.

————. 1949. Investigations in the Geraniaceae. Carnegie Inst. Wash. Yearbook, no. 48: 105–106.

Gärtner, K. F. 1849. Versuche und Beobachtungen ueber die Bastarderzeugung in Pflanzenreich. Stuttgart.

Lanjouw, J. 1939. International cooperation among herbaria and taxonomists. Chronica Botanica 5: 140–150.

Robbins, W. W., Bellue, M. K. and Ball, W. S. 1941. Weeds of California. State Department of Agriculture, Sacramento.

REVIEW

Water in the Physiology of Plants. By A. S. Crafts, H. B. Currier, and C. R. Stocking. xxi + 239 pages, 56 figures, 49 tables, 3 plates, and 4 vignettes. (Volume XXI of A New Series of Plant Science Books edited by Frans Verdoorn.) $6.00. Chronica Botanica Company, Waltham, Massachusetts. 1949.

The appearance during 1949 of two books in the field of plant-water relations serves as a potent reminder of the fact that water is a basic, essential requirement of plants and that it is a major concern of agriculture in many parts of the world. The two books, *Water in the Physiology of Plants* by A. S. Crafts, H. B. Currier, and C. R. Stocking, all of the University of California at Davis, and *Plant and Soil Water Relationships*[1] by Paul J. Kramer of Duke University, Durham, North Carolina, cover—between them—the broad field of water relations including the translocation of solutes, though only passing reference is made to problems of drought and cold resistance.

Water in the soil, the plant, and the atmosphere constitutes a continuous system tending toward equilibrium in all of its parts. Thus, it is difficult to discuss any one part of the system to the exclusion of the rest. This leads unavoidably to a certain amount of duplication in the two books even though the authors were cognizant of each others' effort. One is more impressed, however, with how well they complement each other to give an extremely broad coverage of the field. For this reason both are essential to the plant physiologist. The focal point of Kramer's book is the soil water-root interphase and the factors operative on each side of the boundary with respect to water and solutes. Crafts and his colleagues center attention on the water within the plant and the factors affecting its distribution. Both books discuss the closely related subject of the translocation of solutes. Kramer restricts his treatment to mineral transport in the xylem while Crafts, *et. al.*, include, also, transport in the phloem. Each book has an extensive bibliography thus providing a comprehensive survey of the literature.

Although the book for which this review was requested is *Water in the Physiology of Plants* it seems appropriate to first indicate briefly the contents of both books before passing to a detailed consideration of the one under review. The introductory chapter in each book is followed by a development of the physical-chemical groundwork for considering the water relations of the plant. Crafts, *et. al.*, devote four chapters (about fifty-five pages) to the structure of water, the nature of aqueous solutions and osmosis, and the mechanism of osmosis. Kramer, in his first four chapters of some eighty pages, discusses the nature, movement, measurement, and control of soil moisture.

---

[1] Kramer, P. J. 1949. Plant and Soil Water Relationships. xiii + 347 pp. McGraw-Hill Book Company, Inc., New York.

The plant is now introduced into the picture, the background for the approach to plant-water relations having been laid in each book. Kramer then considers, in order, the structure and growth of roots, the factors affecting the development of root systems, root and stem pressures and exudation phenomena, processes concerned in water absorption, factors affecting the absorption of water, the absorption of solutes, and, finally, absorption deficits and their effects on plants. Crafts and his colleagues continue their book with the intracellular distribution of water, osmotic quantities of plant cells, active cell water relations, uptake and movement of water in plants (including translocation of solutes), concluding with water loss and retention.

Turning now to the book under review (Crafts, *et. al.*), in particular, the two page introductory chapter is a terse summary of source materials, being primarily a bibliography of the classical literature as well as of recent reviews and books in the field of water relations.

Chapter 2 on the structure of water will leave no doubt in the reader's mind that water is far more complex than merely a "mass of spherical molecules, randomly arranged, and independently agitated by thermal energy," but rather, "is composed of polar molecules coordinately arranged in some sort of lattice-like network and bound by a number of intermolecular forces such as dipole attractions, London forces, and hydrogen bonds." Similarly, the next chapter stresses the complexity of aqueous solutions, discussing at length the intermolecular forces between solute and solvent and their effect upon colligative properties. The controversial problem of "bound water" is considered here also.

Consideration of osmosis and the mechanism of osmosis appropriately follows the laying down of working concepts of the nature of water and aqueous solutions. Realizing the dissatisfaction of plant physiologists with the inexact and multitudinous terms in use and the lack of a satisfactory explanation of the mechanism, the authors carefully trace the development of our knowledge of osmosis. They arrive at a set of definitions, liberally illustrated, of the important osmotic quantities and propose a mechanism. Even so, it does not become clear until a later chapter that osmotic pressure includes all factors, not just solute alone, which reduce the diffusion pressure of water. Similarly, the broad meaning of turgor pressure is not clear until a later chapter. The terminology adopted is that recommended by the Physical Methods Committee of the American Society of Plant Physiologists. These authors also postulate a mechanism for the kinetic interpretation of osmosis. I doubt that the arguments over mechanism and terms will be resolved by the treatment given here; however, the terminology seems destined to become universal in the United States, since most students are being exposed to it.

The next two chapters, VI and VII, include the distribution of water in cells, i.e., its distribution between cell wall, protoplasm, and vacuole, and methods for measuring osmotic pressure and diffusion pressure deficit. After this treatment of the water movement between cells as a strict osmotic phenomenon, it becomes necessary here—as in other recent articles—to evaluate the evidence indicating that the protoplasm is not passive with respect to the passage of water, but plays some vital role in water distribution. They conclude, after a lengthy discussion in Chapter VIII, that the evidence is inconclusive.

Chapter IX is concerned with the absorption of water by roots and the translocation of water and solutes. A curious duality in the use of terms becomes apparent in this chapter. Here, "active absorption" is considered to be the osmotic entrance of water from the soil solution into the xylem resulting (under appropriate conditions) in a root pressure. "Passive absorption," on the other hand, is a similar movement, but one in which the diffusion pressure deficit in the xylem is due to tension rather than solute. This conflicts with the definitions in the earlier chapter on the active uptake of water by cells, where the metabolic absorption of water is considered to be the "active absorption" while "passive absorption" is the osmotic entrance of water. After the evaluation of the evidence and the discussion of methods for the "movement of water through the plant, there is an extended fine-print section on the translocation of solutes. Concerning the flow of food, viruses, indicators, etc., they state, "The simplest and most compatible mechanism to account for such flow would seem to be mass flow along hydrostatic gradients developed osmotically." It seems to me that, in view of equally valid data which are incompatible with the mass flow concept, it is illogical to support a theory because it is "simple and most compatible," if it does not fit all of the facts.

The concluding chapter of this book discusses the researches on transpiration, stomatal behavior and mechanisms, subaqueous transpiration, and the effects of water deficits.

I trust that this review indicates, as does the book, that the field of plant-water relations is far from a closed subject. Unsolved problems await the investigator even on such issues as terminology and mechanism of osmosis, to say nothing of the complexities of water relations within the plant. This book provides a logical and comprehensive insight into the complex and extensive field of plant-water relations. Leonard Machlis, Department of Botany, University of California, Berkeley.